

## THE NERVOUS SYSTEM OF PELAGIC NEMERTEANS.

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During the past ten years a considerable number of species of bathypelagic nemerteans have been studied anatomically by Brinkmann ('17) and others and much information has been secured, showing the deviations of the nervous system from the general plan characteristic for the littoral forms. Five new genera, collected by the "Albatross" in various parts of the Pacific ocean, which have recently been fully studied by the writer (Coe, '26), proved of particular interest in this respect. One of these species, *Neuronemertcs aurantiaca*, possesses a chain of ganglia along the dorsal nerve, a condition almost unique in invertebrates.

In the modifications of the sense organs also the pelagic nemerteans (Pelagica) differ widely from any of the littoral and bottom-living species (Reptantia).

It is to be recalled that bathypelagic nemerteans have been found only in the open oceans, where they swim with sluggish movements or float idly, but always far beneath the surface. Certain of the species are known to be restricted to particular water layers, usually at depths of from 500 to 1,500 meters, and presumably all the species are limited in their vertical range by the conditions of temperature and salinity, and to some extent, perhaps, by the pressure, to which they have become specifically adapted. Their geographical range, on the other hand, may be very wide, since water layers of essentially similar physical and chemical properties extend through vast areas of the oceans and almost from pole to pole. It is in conformity with these environmental conditions that the bathypelagic organisms have evolved.

Up to the present time 47 species of these aberrant worms have been described, but it is quite possible that some of them may be synonyms. More than half of them have been carefully studied with respect to their anatomical peculiarities, including those of the nervous system. Stiasny-Wijnhoff ('23) has also described

a form which was taken from the bottom at a depth of 833 meters, which is in some respects intermediate between the Pelagica and the Reptantia.

*Brain.*—In Fig. 1 a general plan of the nervous system is shown. The brain of the pelagic forms is essentially similar to that of the littoral species, but as a rule the dorsal ganglia are considerably smaller than the ventral. The two ganglia of each side are closely fused together. The fibrous cores and the three types of ganglion cells are also similar, but neurochord cells have not been found in any species.

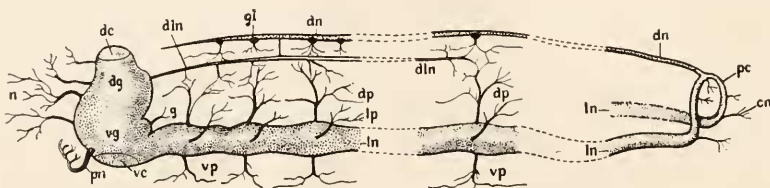


FIG. 1. Diagram of nervous system of *Neuronemertes aurantiaca* Coe, showing relation of brain and lateral nerves (*ln*) to peripheral nervous system; *dg*, dorsal, and *vg*, ventral ganglia of brain; *dc* and *vc*, the corresponding commissures; *n*, cephalic nerves; *g*, gastric nerve; *pn*, proboscis nerve; *dn*, dorsal nerve, with metameric ganglia (*gl*); *dln*, dorsolateral nerve; *dp*, *lp*, *vp*, dorsal, lateral and ventral peripheral nerves, respectively; *pc*, posterior commissure; *cn*, caudal nerves.

One of the most striking peculiarities of the pelagic forms is the great amount of gelatinous tissue, or parenchyma, which surrounds all the internal organs, giving the body a high degree of permeability and a low specific gravity, enabling the worms to float freely in the water at great depths with a minimum of muscular exertion. This parenchyma surrounds the brain and usually separates it widely from the thin musculature of the head.

The probosis passes through the ring made by the ganglia and their dorsal and ventral commissures, while the stomach lies beneath the ventral commissure in most species.

Three longitudinal nerve stems extend the entire length of the body; the pair of lateral nerves, situated in the body parenchyma beneath the intestinal diverticula, and the median dorsal nerve, which lies directly beneath the basement layer of the epidermis. The former are direct continuations of the ventral brain lobes, while the dorsal nerve has no direct connection with the brain

(Fig. 1). The fibrous cores of these main nerves are connected at the posterior end of the body by the broad posterior commissure, which passes on the dorsal side of the rectum. They are also connected indirectly metamerically by the union of minute branches from both dorsal and dorsal peripheral nerves in the intermuscular plexus (Figs. 1, 2, 4).

*Dorsolateral nerves.*—In the anterior part of the body of many of the species studied a pair of nerves originating from the dorsal

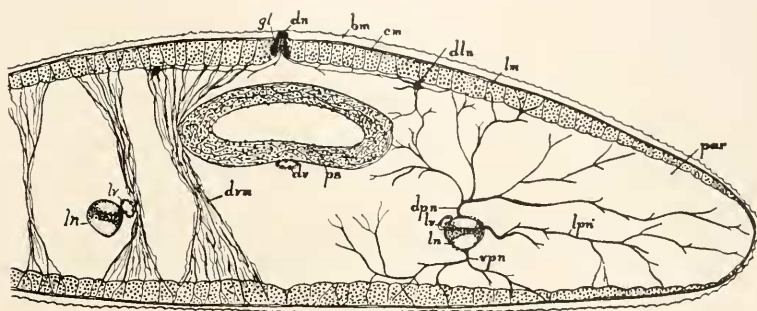


FIG. 2. Portion of transverse section of body of *Neuronemertes aurantiaca* Coe, showing on one side the relations of the peripheral nerves to the body musculature. The section passes between adjacent diverticula of the intestine and shows on the left hand side a portion of the dorsoventral musculature (*dvn*); *dn*, dorsal nerve, with bilobed ganglion (*gl*); *dpn*, *lpn*, and *vpn*, dorsal, lateral and ventral peripheral nerves; *ps*, proboscis sheath; *dv* and *lv*, dorsal and lateral blood vessels; *bm*, basement layer underlying the surface epithelium; *par*, parenchyma; *cm* and *lm*, the thin circular and longitudinal musculatures of the body walls. Other letters as in Fig. 1.

brain lobes, pass backward along the internal border of the body musculature near the dorsolateral edges of the proboscis sheath. These dorsolateral nerves (Figs. 1, 2) are connected by means of delicate fibres with both the dorsal nerves and the dorsal peripheral nerves of the lateral nerve cords. Efferent branches supply the body musculature on the dorsolateral aspects of the body, as well as the proboscis sheath. These nerves are evidently homologous with the dorsolateral nerves of other Platyhelminths. They do not occur in all the pelagic species, and where present are limited to the anterior end of the body (Fig. 1). In other species, and toward the middle of the body in all species, their place is taken by fibres from the dorsal peripheral nerves.

*Dorsal nerve.*—This nerve appears to represent a local concentration of fibers from the dorsal peripheral nerves, for it is not connected directly with the brain, so far as known, in any of the pelagic forms. It extends in the median line and just external to the circular muscular layer, joining the commissure of the lateral nerves at the posterior end of the body. When followed forward toward the brain it becomes gradually smaller and finally terminates in the cephalic parenchyma or in the delicate intermuscular plexus a short distance posterior to the dorsal brain commissure (Fig. 1).

Fibers from the dorsal nerve supply the dorsal musculature and integument of the body. Other fibers enter the nervous plexus lying between the two muscular layers, while still others are connected with the dorsolateral and dorsal peripheral nerves.

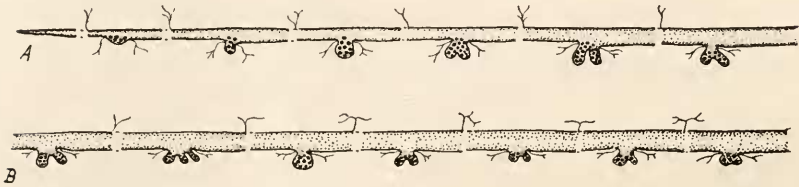


FIG. 3. *A*, Diagram of anterior end of dorsal nerve with its accompanying ganglia, showing variations in shape of the latter and the minute fibrils which pass dorsally into the integument and ventrally into the intermuscular plexus. *B*, Similar diagram from near middle of body.

*Ganglia of dorsal nerves.*—In most species only a few scattered ganglion cells are to be found along the course of the dorsal nerve, but in *Neuronemertes aurantiaca* this nerve is very large and is provided with a series of nervous structures, apparently of the nature of ganglia, although such organs have not hitherto been found in any species of nemertean. In my monograph on the Pelagic Nemerteans (Coe, '26) they were referred to as "problematical organs" although their probable nature as ganglia was emphasized (p. 130).

The number of these organs is upward of a hundred, corresponding presumably to a primitive metamerism.

Anteriorly the ganglia are somewhat smaller than the diameter of the fibrous core of the dorsal nerve, but farther back in the body they are several times as large as the nerve and are often

divided into two or more lobes (Figs. 3, 4). The nerve itself lies external to the circular muscular layer, while the ganglia are internal to these muscles and interposed between the bundles of longitudinal muscles. The broad connection between ganglion and nerve therefore requires the penetration of the thin circular musculature. This is accomplished by the mere separation of adjacent circular fibers so as to leave a narrow slit through which the connection passes.

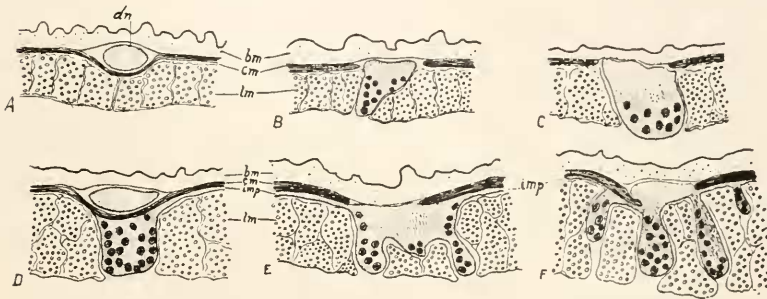


FIG. 4. Transverse sections of six of the ganglia of the dorsal nerve of *Neuronemertes aurantiaca* Coa, showing variations in shape and their relations to the nerve core. *A*, Dorsal nerve between two adjacent ganglia. *B*, Small ganglion closely fused with dorsal nerve. *C*, Large ganglion with ventral group of nerve cells. *D*, Surface view of ganglion, its connection with dorsal nerve being in an adjacent section. *E*, Large ganglion with three lobes of nerve cells and distinct intermuscular plexus. *F*, Large ganglion with four lobes of nerve cells; *imp*, intermuscular plexus; other lettering as in Fig. 2.

The cells composing the ganglia are similar in size and appearance to those which accompany the lateral nerve cords, and the cell boundaries are likewise rarely to be distinguished (Fig. 4). It has been difficult to determine the precise nature of these organs. That their component cells are the source of fibers which innervate the integument and musculatures seems highly probable. And it is also presumable that they supplement the nerve cells found in all species accompanying the lateral nerve cords, but there is no evidence that these latter cells are less abundant in this species than in other pelagic forms. A suggestion that may have some degree of plausibility is that they are associated with the great development of the dorsoventral musculature, particularly in the region where the spermaries are situated in the male,

just behind the head. In *Neuronemertes* the walls of the spermaries are not provided with the thick spiral musculature found in several other pelagic forms and which serves to supplement the weak muscles of the body walls in the forcible discharge of the spermatozoa. A similar result is accomplished however by the contraction of the highly developed dorsoventral muscles which closely invest the spermaries in that genus. It therefore seems reasonable to suspect that these supplementary nervous tissues may function in the control of this dorsoventral musculature throughout the body.

There still remains the possibility of the ganglia being correlated with sensory stimuli rather than with motor responses, but their structure is unlike that of any known receptor. It seems necessary, therefore, to return to the view that the ganglia of the dorsal nerve supplement the nerve cells of the lateral nerve cords just as these supplement those of the brain.

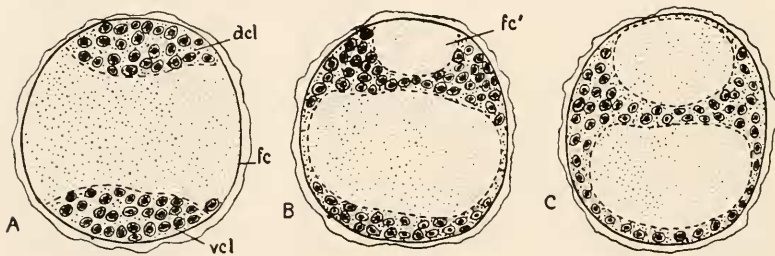


FIG. 5. Transverse section of lateral nerve cord in three different genera, showing the relations of the fibrous cores to the accompanying nerve cells. A, *Plionemertes plana* Coe, with single fibrous core (*fc*) and symmetrical dorsal and ventral cellular layers (*dcl* and *vcl*); B, *Proarmaueria pellucida* Coe, with small dorsal core (*fc'*); C, *Planonemertes lobata* Coe, with large dorsal core.

*Lateral nerves.*—These are direct continuations of the fibrous cores of the brain lobes and are accompanied by nerve cells throughout their entire length. At the posterior end of the body the cords of the two sides form a broad commissure on the dorsal side of the rectum (Fig. 1). In most pelagic species the fibrous core arising from the dorsal brain lobe is separated by a layer of ganglion cells, at least in the anterior part of the body, from that arising from the ventral lobe of the brain (Fig. 5).

The dorsal core is much smaller than the ventral and its separation from the latter tends to become less distinct in the posterior half of the body. Toward the posterior end of the body this core becomes gradually smaller, only the fibers of the ventral core being involved in the posterior nerve-commissure.

In a few genera there is but a single fibrous core, and this arises mainly from the ventral ganglion. It presumably also contains fibers from the dorsal ganglion, although they are usually not visibly separated from the others (Figs. 5, 8).

The position which the lateral nerves occupy in the body varies greatly according to the degree of development of lateral margins. In those forms in which the body is but little flattened, the nerve-cords lie near the lateral margins of the body, but in the broad, flattened forms they are far removed from the lateral margins, being in some cases situated more than half-way toward the median line (Fig. 6). In nearly all species the nerve-cords bend more or less sharply laterally immediately after their origin from the brain. In most forms they lie in the parenchyma near the ventral surface of the body, but in those cases where large ventral branches from the intestinal diverticulum force their way beneath the nerve-cord, the latter is moved dorsally until it may lie about midway between dorsal and ventral surfaces (Fig. 6).

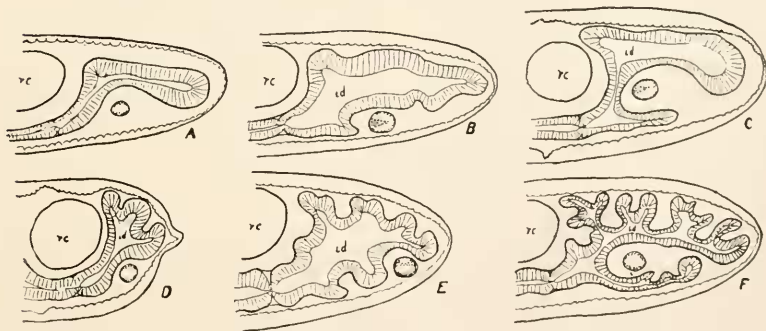


FIG. 6. Portions of transverse sections of body of six different genera, showing the position of the lateral nerve cord with respect to the body walls and intestinal diverticula. *A*, *Pelagonemertes joubini* Coe; *B*, *Planonemertes lobata* Coe; *C*, *Neuronemertes aurantiaca* Coe; *D*, *Cuneonemertes gracilis* Coe; *E*, *Nectonemertes pelagica* Cravens and Heath; *F*, *Planktonemertes agassizii* Woodworth.

*Nerve cord muscle.*—In the genera belonging to the families *Armaueriidae* and *Pelagonemertidae* and in *Pendonemertes* of the *Protopelagonemertidae* a narrow band of muscular fibers splits off from the proboscis sheath on each side of the body immediately back of the brain and extends backward throughout the length of the body in close connection with the lateral nerve cord. In some forms it lies close against the outer connective sheath on the median face of the nerve cord, while in other cases it penetrates the sheath and comes to lie in close connection with the nervous tissues. This muscle is usually very thin, consisting of only one or two layers of muscular fibers (Figs. 7, 8A), but in a few species it is so large that it equals fully half the diameter of the nerve cord itself (Fig. 8B).

In *Pelagonemertes joubini* the muscle leaves the proboscis sheath as several separate strands (Fig. 7) and these may at first take separate positions on the face of the nerve cord, but further back in the body they fuse into a single flattened bundle.

The function of the nerve cord muscle is evidently to hold the nerve cord in position with reference to the organs which the latter innervates.

*Peripheral nerves.*—As a rule three peripheral nerves leave each lateral nerve cord in each of the spaces between adjacent intestinal diverticula. One of these three nerves, dorsal peripheral, leaves the dorsal side of the cord (Figs. 1, 2, 7, 8) to supply the dorsal musculature and integument and in some cases the proboscis sheath (Figs. 2, 7). This nerve also sends branches into the intermuscular plexus and indirectly connects with the dorsal and dorsolateral nerves. Small branches also supply many of the dorsoventral muscles.

The lateral peripheral is a slender nerve with few branches. These supply the lateral margin of the body and appear also to enter the intermuscular plexus (Figs. 2, 7).

The ventral peripheral originates from the ventral core of the cord and divides into two branches which supply the ventral portions of the body. Branches from this nerve also enter the ventral intermuscular plexus (Figs. 1, 2, 7, 8).

*Intermuscular plexus.*—In some of the sections of *Neurone-  
mertes aurantiaca* distinct nerves can be seen leading from the

dorsal nerve inward through the circular muscular layer and thence laterally between the two muscular layers of the body-walls. These nerves appear to constitute part of a great plexus

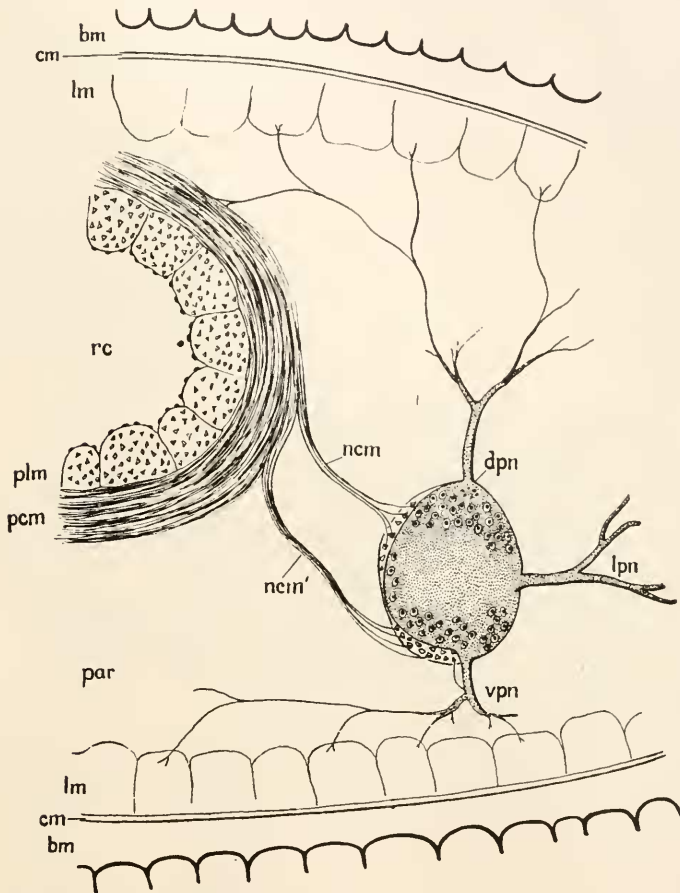


FIG. 7. Diagram of portion of transverse section of body of *Pelagoneurtes joubini* Coe, immediately posterior to the brain, showing origin of the nerve cord muscles (*ncm*, *ncm'*) from the outer spiral musculature of the proboscis sheath, and the three main branches, dorsal (*dpn*), lateral (*lpn*), and ventral (*vpn*) which leave the nerve cord in each interdiverticular space; *rc*, rhynchocoel; *plm* and *pcm*, longitudinal and circular-spiral muscular layers of proboscis sheath; other lettering as in Fig. 2.

of nerve-fibers which extends between the circular and longitudinal musculatures throughout the length of the body, both

dorsally and ventrally (Fig. 4). The plexus is in frequent communication with the peripheral nerves from the lateral cords, as well as with the dorsal and dorsolateral nerves.

*Tentacular nerves.*—The adult males of *Nectonemertes* and both sexes of *Balanemertes* are each provided with a pair of tentacles immediately back of the head. These appendages are lateral outgrowth of the body walls and are supplied with large nerves homologous with the lateral peripheral nerves in other parts of the body (Fig. 9).

*Proboscis-sheath nerves.*—In many pelagic species the proboscis sheath is supplied with nerves which enter it at the ring where the proboscis is attached, but in other forms the organ also receives one or more pairs of fine branches from the dorsal peripheral nerves (Figs. 2, 7).

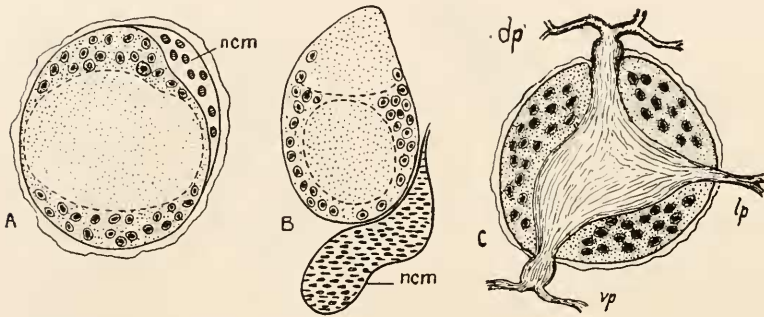


FIG. 8. *A*, Transverse section of lateral nerve cord and accompanying muscle (*ncm*) in *Cunconemertes gracilis* Coe. *B*, Same in *Balanemertes chuni* Bürger. *C*, Section of lateral nerve cord in *Planktonemertes agassizii* Woodworth, showing the origin of dorsal lateral and ventral peripheral nerves.

*Proboscidial nerves.*—The proboscis is large and highly specialized in most of the pelagic nemerteans, with a powerful musculature and a thick epithelial lining of secretory and sensory cells in addition to the minute sickle-shaped weapon with which it is provided. Consequently it requires an abundant supply of nerves. In some forms these are provided by means of a pair of large nerve stems arising from the points where the ventral commissure joins the ventral brain lobes (Fig. 1). This pair of large nerves divides into the definite number of proboscidial nerves

either at the attachment of the proboscis or in the organ immediately posterior to its insertion. But in other forms, where the proboscis is inserted close in front of the brain, the proboscidal nerves either arise in the complete number from the ventral brain lobes and the commissure adjacent or branch immediately after their origin.

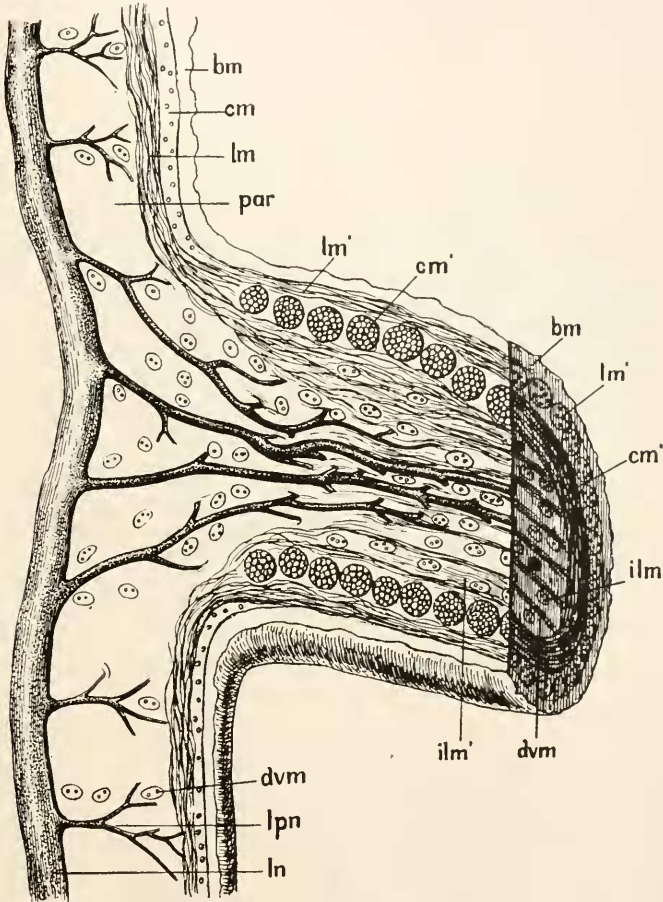


FIG. 9. Diagram of portion of horizontal section of tentacle and adjacent body wall of *Nectonemertes mirabilis* Verrill, showing the four large tentacular nerves originating from the lateral nerve cord (*ln*). These are homologous with the lateral peripheral nerves (*lpn*) of the rest of the body; *bm*, basement layer underlying the surface epithelium; *lm*, longitudinal and *cm*, circular muscular layer; *ilm*, internal longitudinal muscles; *dvm*, dorsoventral muscles; *par*, parenchyma.

The nerves take up a position in the midst of the longitudinal muscular layer along the whole circumference of the proboscis (Fig. 10). This position varies somewhat in the different forms, but is generally about two thirds the distance from the inner to the outer border of the longitudinal muscular layer. Here the nerves branch out to form a thick plexus of connecting fibers and send symmetrical branches radially both towards the periphery and towards the glandular epithelium lining the central lumen (Fig. 10).

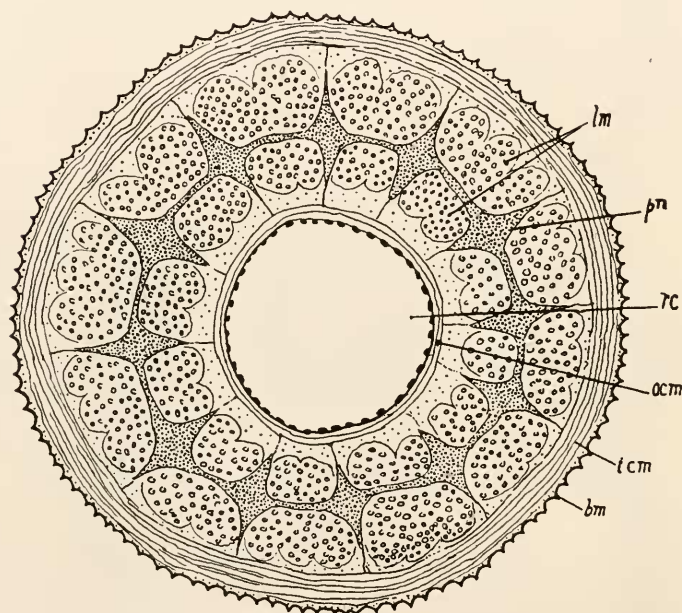


FIG. 10. Transverse section of everted proboscis of *Cuneonemertes gracilis* Coe, with the 12 proboscic nerves (*pn*) connected by a plexus in the midst of the longitudinal muscular layer (*lm*); *lcm* and *ocm*, inner and outer circular musculatures; *bm*, basement layer underlying the inner, glandular epithelium; *rc*, extension of the rhynchocoel; lined with endothelium.

About midway between each two proboscic nerves in certain species the plexus is condensed into a secondary nerve, commonly about half the diameter of one of the main nerves. There is thus an equal number of primary and secondary nerves in such species. In some forms it is difficult to distinguish the two sets

of nerves, so that one specimen may appear to have double the number found in other specimens where the proboscis is in a different state of contraction. Furthermore in some forms the number of nerves in the anterior end of the proboscis may be double that found farther back toward the stylet region, due to the gradual disappearance of each alternate, or secondary, nerve in the plexus. And, finally, the number may vary to some extent in different individuals, as in *Nectonemertes mirabilis* where the number ranges from eighteen to twenty-four.

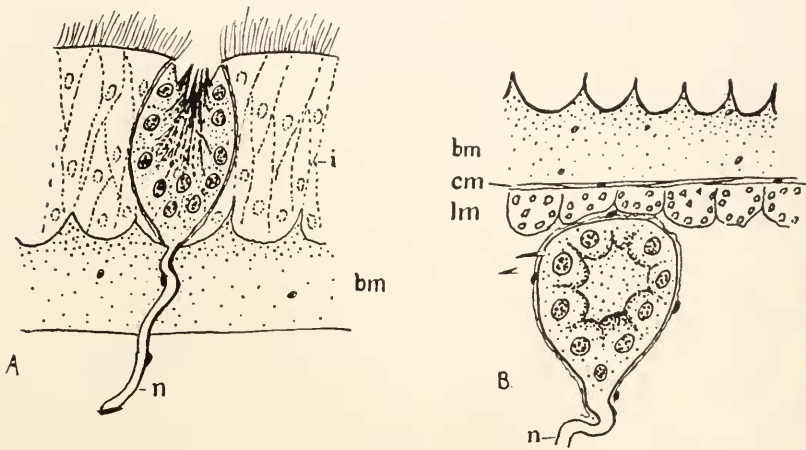


FIG. 11. Diagrams of the two types of sense organs found in *Cunconemertes gracilis* Coe. A, integumentary sense organ; B, subcutaneous sense organ; bm, basement layer of surface epithelium (i); cm and lm, circular and longitudinal musculatures of cephalic wall; n, nerve leading to dorsal brain lobe.

The central radial branches from the nervous plexus pass between the bundles of longitudinal muscles and form a second, delicate intermuscular plexus beneath the inner circular muscles. From this plexus fine nerve-fibers supply the epithelium of the papillæ as well as the inner circular muscles.

The peripheral radial branches arising from each of the primary nerves form a third, still more delicate, plexus between the longitudinal muscles and the outer circular muscular layer. This supplies in a similar manner the more superficial layers of the proboscis, namely, the outer circular muscles and the endothelium.

Of the three nervous plexuses (middle, inner, and outer) which are thus formed the two latter are of such great delicacy that they can be observed only under favorable conditions of preservation, and it is by no means certain that they are present in all species.

Although the radial nerves leave the middle plexus only at intervals, the three plexuses appear to form more or less continuous networks throughout the length of the anterior chamber. In some forms even the middle plexus is incompletely developed, the primary proboscidial nerves being connected with each other only at intervals.

The plexuses are interrupted in the middle chamber of the proboscis by the interlacing of the muscular layers, and the primary nerves gradually lose their identity in a multitude of smaller branches, some of which innervate the stylet musculature and gland-cells, while others continue backward into the wall of the posterior chamber. Hence in the posterior chamber the primary nerves are not usually distinguishable as separate units and there is but a single plexus lying between the longitudinal muscles and the glandular epithelium lining the lumen.

The smallest number of proboscidial nerves found in any pelagic species is 7, and the largest is 50, the most frequent numbers being from 15 to 25. In general, the species in which the individuals attain the largest size have a greater number than those in which the animals are but a few millimeters in length. Odd and even numbers are about evenly distributed.

*Cephalic nerves.*—The muscles, integument and sense organs of the head are supplied with a considerable number of fine nerves which arise from the anterior surfaces of both dorsal and ventral brain lobes (Fig. 1). But since the cephalic musculature is extremely weak and the sense organs rudimentary, the cephalic nerves are very much smaller than in most other nemerteans.

*Gastric nerves.*—A pair of small nerves arise from the posterior end of the ventral brain lobes to supply the anterior end of the digestive tract (Fig. 1). These are homologous with the esophageal nerves of the littoral forms which have the esophagus well developed, but where that part of the digestive system is rudimentary, as in the pelagic species, the nerves supply the stomach. Supplementary gastric nerves, originating from the ventral commissure, have also been observed in one or more species.

*Pyloric nerves.*—In some species, at least, a pair of minute nerves, originating from the lateral nerve cords, enters the anterior end of the pylorus.

*Caudal nerves.*—The posterior extremity of the body is supplied with nerves in two different ways. In *Proarmaueria* the posterior end of each of the lateral nerves divides into two branches, the larger of which enters the posterior commissure, while the smaller supplies the extremity of the body. In *Neurone-mertes* and some other forms the caudal extremity is supplied with small nerves from the commissure itself (Fig. 1).

*Sense-organs.*—Even the most primitive of the littoral nemerteans are provided with special sense-organs as differentiated portions of the integument, and in the higher groups ocelli, cerebral sense-organs, and frontal sense-organs are of frequent occurrence. In addition, otocysts are found in a few species. But in the pelagic forms no such organs have been found in any of the species studied. Possibly vestiges of one of these types of sense-organs were discovered by Bürger ('09) in *Balananemertes*. These are considered by him to be rudimentary ocelli, and similar organs were shortly afterward found by Brinkmann in *Pelagonemertes rollestoni*. Further studies have shown them to be widely distributed among the *Armaueriidae* and *Pelagonemertidae*. They are of two distinct types, as follows:

*Subcutaneous sense-organs.*—In these forms a small cluster of sense-organs, whatever their nature may be, is situated beneath the basement layer of the anterior margin of the head, frequently on either side of the rhynchodeal opening. Each of the end-organs consists of a pear-shaped group of cells, connected with a branch of one of the cephalic nerves (Fig. 11B). Some of them lie in contact with the inner border of the basement-layer, while others may be situated somewhat deeper in the cephalic tissues, and in or even beneath the muscular layers. Since they differ widely from typical nemertean ocelli in structure, it seems quite possible that these may be special sense-organs peculiar to the pelagic forms rather than that they represent degenerate ocelli.

*Integumentary sense-organs.*—A second type of sense-organ occurs in the integument of the head and less frequently in other parts of the body in certain genera. These consist of compact

groups of sensory cells imbedded in the integument. The cells are provided with slender distal processes and each group is supplied with a nerve leading to the brain or to the lateral nerve, according to its location (Fig. 11A). It is not improbable that such integumentary sense-organs occur in the majority of the pelagic species, but that the loss of the integument during capture has prevented their discovery.

#### SUMMARY.

Correlated with their usually gelatinous consistency, weak musculature and other adaptations for life far beneath the surface of the oceans, the nervous system of the bathypelagic nemerteans (Pelagica) differs considerably from that found in the littoral and bottom-living relatives (Reptantia). Comparisons are made between the Pelagica and Reptantia with respect to each of the principal parts of the nervous system. The special sense-organs of the Reptantia are either lacking entirely or merely vestigial in the bathypelagic forms. With particular reference to a recently described species, *Neuronemertes aurantiaca*:

1. The dorsal nerve is not connected directly with the brain.
2. The dorsal nerve is provided with metameric ganglia, not previously known for any nemertean.
3. A pair of dorsolateral nerves connects both with the dorsal nerve and with dorsal peripheral branches of the lateral nerve cords.
4. A delicate intermuscular plexus lies between the two body musculatures.

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